

Evidence of Parental and/or Sibling Manipulation in Three Species of Termites in Hawaii (Isoptera)¹

TIMOTHY G. MYLES²

ABSTRACT

Wing pad and leg scars are reported to occur on three of the four species of termites found in Hawaii: *Cryptotermes brevis* (Walker), *Incisitermes immigrans* (Snyder), and *Neotermes connexus* Snyder (Kalotermitidae). Such scars were not found on *Coptotermes formosanus* Shiraki (Rhinotermitidae). The nature, placement and frequency of scars all support the view that such scars are inflicted by nestmates and are not due to physical accidents or attacks by heterospecifics. These are the first records of nestmate manipulation for all three genera and the first such records for the Oceanic region. This is also the first report of manipulation by leg biting and the first report of leg regeneration in the Isoptera. Scarring appears to be the determinative event in pseudo-worker differentiation in many lower termites.

All termites are eusocial (Wilson, 1971). Eusocial species are usually characterized by the self-sacrificing features of their biology such as sterile castes and altruistic soldiers. Thus, it may seem surprising that termites sometimes behave in selfish, manipulative, and even lethal ways toward their nestmates (e.g. neotenic siblicide, see Myles and Chang, 1984; Myles, 1985). Criticism of the validity (or potency) of colony level selection has led sociobiologists to re-examine animal social groups and attempt to reinterpret social interactions and social structure in terms of individual level selective value. Such thinking has recently led some termite biologists to reconsider the meaning of scars. Several early investigators noted wing pad scars on termites (Grassi and Sandias, 1896; Imms, 1919; Banks and Snyder, 1920; Thompson, 1922; Heath, 1927). However not until Springhetti (1969) were scars considered to be anything other than accidental and maladaptive.

Springhetti's study of the dry wood termite of southern Europe, *Kalotermes flavicollis* (Fabricius), showed that wing pad and leg scars led to regressive molting. He suggested that this might be adaptive at the colony level by preventing or delaying the maturation of some individuals into alates, thereby enlarging the colony's work force (kalotermitids have no "true" worker caste but regressive and stationary molting individuals are called pseudergates or pseudoworkers (Noirot, 1985)). Zimmerman (1983) discovered that about 10% of individuals of an Arizona kalotermitid, *Pterotermes occidentis* (Walker), have mutilated wing pads. He postulated that the scars are inflicted by siblings rather than by reproductives. He suggested that a colony's initial pseudergates are pheromone-induced and that these bite others to "recruit" them to the work force so as to improve their own indirect fitness. Sewell and Watson (1982) also noted wing pad scars in the Australian *K. banksiae* Hill.

As another of many remarkable instance of convergence between ants and termites, worker-inflicted bite scars have been reported on larval thoraces of the ant, *Myrmica ruginodis* (Brian and Hibble, 1963). Workers only bite large larvae destined to become gynes; and biting has the effect of switching these larvae toward worker development (Brian, 1973). Wilson (1971:335) has termed this phenomenon "altruistic selfishness."

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²Department of Entomology, University of Arizona, Tucson, Arizona 85721.

It would be of interest to know how widespread scarring is in termites. As part of a larger study to investigate the phenomenon (to be published elsewhere) I have examined samples of preserved material of all four of the species in Hawaii. The frequency data for the three Hawaiian species with scars is presented in Table 1. Examples of recent and healed scars for the three species are shown in Figures 1-3.

None of the above investigators actually observed termites in the act of biting nestmates. This raises the question of whether scars might have other causes. Once the scars are closely examined the possibility that they might arise by physical accidents seems nearly impossible. The scars under consideration have a characteristic appearance and fairly uniform placement. Scars due to rough handling of termites during extraction from wood are irregular in appearance and easily distinguishable. Wing pad scars typically have the cuticle mangled and twisted, occasionally leaving a small corner of the cuticle torn. The wounded area discolors from castaneous to black. The scars are regularly positioned on the posterior lateral margins of the pteronota (rarely the pronotum or basal abdominal segment) (see Fig. 2, 3A & 3C). Many mid-developmental stages have asymmetrical wing pads suggesting scarring in earlier instars (Fig. 3C). Leg scars typically are clean truncations

TABLE 1. Frequency data on wing pad and leg scars of species of termites occurring in Hawaii. Note that the sample of *C. brevis* was collected in Florida.

Species	Collection information	scar data*
<i>Cryptotermes brevis</i>	Key Largo, Florida board in abandoned house Dec. 7, 1985 T.G. Myles & M.S. Collins	of 284: 10 with pad scars 3 with asymm. wing pads 26 with leg scars 16 with regen. legs Total: 55/284=19.4%
<i>Incisitermes immigrans</i>	1) Honolulu, Hawaii dead branches 1980 T.G. Myles 2) Kipu, Kauai Jul. 22, 1966 R.C.A. Rice (W.L. Nutting collection)	of 13: 2 with leg scars of 130: 6 with wing pad scars 2 with leg scars 1 with regen. leg Total: 11/143=7.7%
<i>Neotermes connexus</i>	1) Honolulu, Hawaii <i>Leucana glauca</i> 1978-1981 T.G. Myles 2) same	of 451 mixed stages: 10 with wing pad scars 9 with asymm. wing pads 28 with leg scars 3 with regen. legs of 152 mixed stages: 14 with wing pad scars 3 with asymm. pads 2 with leg scars

Continued on next page.

at the level of the coxa (Fig. 1A & 1B) or trochanter (Fig. 3B). A black scab forms over the wound. Leg stubs and miniature legs about 1/4 or 3/5 the normal length suggest that legs can be nearly fully regenerated within three molts (Fig. 1C, 1D, 3D). These observations strongly suggest biting of some sort.

The possibility that such scars might be inflicted by heterospecifics such as ants has not previously been considered. It is conceivable that some ubiquitously associated predator might employ such scarring to manipulate the termites to its advantage. Similar "animal husbandry" type interactions occur between some ants and aphids. Such an interpretation was seemingly lent support by the occasional finding of *Crematogaster* sp. and *Forelius* (?) sp. ant head attached to the appendages of *Pterotermes* (in over 100 colonies censused only 9 examples were found: 5 to mid-tibiae, 2 to antennae, 1 to abdomen, and 1 to labium, personal observation). The nature and placement of these known ant-inflicted scars do not match the wing pad and leg scars that are so commonly found.

Another argument against heterospecifics as agents of scarring derives from the immigrant status of Hawaii's fauna. If scars are inflicted by predators in continental regions, then one might expect Hawaii's immigrant termite species (Zimmerman, 1948) to have escaped such predators and be free of scars. This seems a reasonable supposition, especially in view of the depauperate nature of the ant fauna. No ants were found associated with termites in Swezey's (1954) extensive survey of the

Table 1 continued.

Species	Collection information	scar data*
<i>Neotermes connexus</i> (cont.)	3) same	of 343 N2 & N3 nymphs: 24 with wing pad scars 7 with asymm. pads 6 with leg scars 2 with regen. legs
	4) same	of 289 soldiers: 18 with wing pad scars 6 with asymm. pads 5 with leg scars 2 with regen. legs
	5) same	of 215 alates: 5 with leg scars 1 with regen. leg
	6) same	of 69 neotenics: 4 with wing pad scars 9 with asymm. pads 3 with regen. legs
Total:		161/1649=9.8%

*Also included under pad scars are occasional scars to pronotum or basal abdominal segment. Only grossly asymmetrical wing pads were counted under asymm. pads. Leg scars includes all leg truncations most of which occur at the trochanter, not included are tarsal scars and leg joint scars which are also common. Antennal and palpal scars occur but were not tallied.

forest insects of Hawaii. The fact that scars occur that are very similar to those found on continental kalotermitids supports the view that scars are inflicted by nestmates.

Studies of leg regeneration in other insects have shown that distal regeneration can occur at any level of the tarsus or tibia but that the femur lacks regenerative ability (Bullière and Bullière, 1985). They also showed that amputations at different levels of the femur result in autotomy at the trochanter-femur articulation. These generalizations appear to apply to termites since regenerations from different levels of the tibia were found but whenever the femur was involved the regeneration arose from the trochanter or coxa (Fig. 1C & 1D). The prevalence of leg truncation scars at the level of the trochanter may also be explained by autotomy rather than indicating leg biting at that level (Fig. 3B).

I hope this paper will stimulate entomologists in Hawaii to collect whole colonies of kalotermitid termites in order to obtain more information on scarring and the role it plays in the social biology of lower termites. Many questions about this phenomenon remain unanswered. Which individuals or castes inflict the scars? In addition to determining pseudergate differentiation does scarring bias individuals toward neotenic or soldier development? Why does scarring sometimes occur on soldiers and neotenics who have already reached their terminal stage of development? What regulates the frequency of scarring? What are the fitness effects of scarring on the biter, the victim, and the colony? Are the causes and effects of wing pad biting different from leg biting? Since legs are probably of some nutritional value, might they be, in effect, "trophic legs" analogous to the trophic eggs of ants (the pun was irresistible but the question is asked in all seriousness)? Lastly, to what extent is termite sociality founded on handicapped labor?

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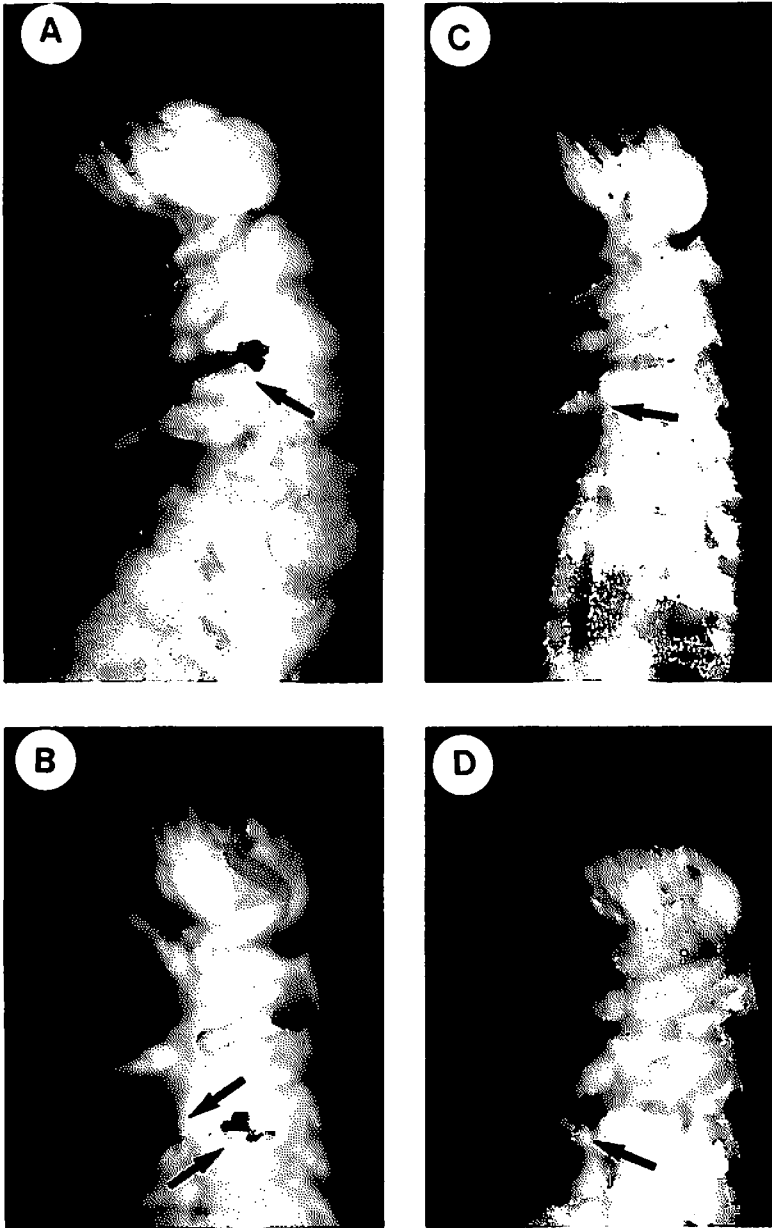


FIGURE 1. A-D. *Cryptotermes brevis*: A, leg truncation scar to left mesothoracic base of coxa of nymph; B, two leg truncation scars to bases of metathoracic coxae of larva; C, regenerated right metathoracic leg stub on larva (probably one molt since leg truncated); D, regenerated miniature right metathoracic leg (probably two molts since leg truncated).

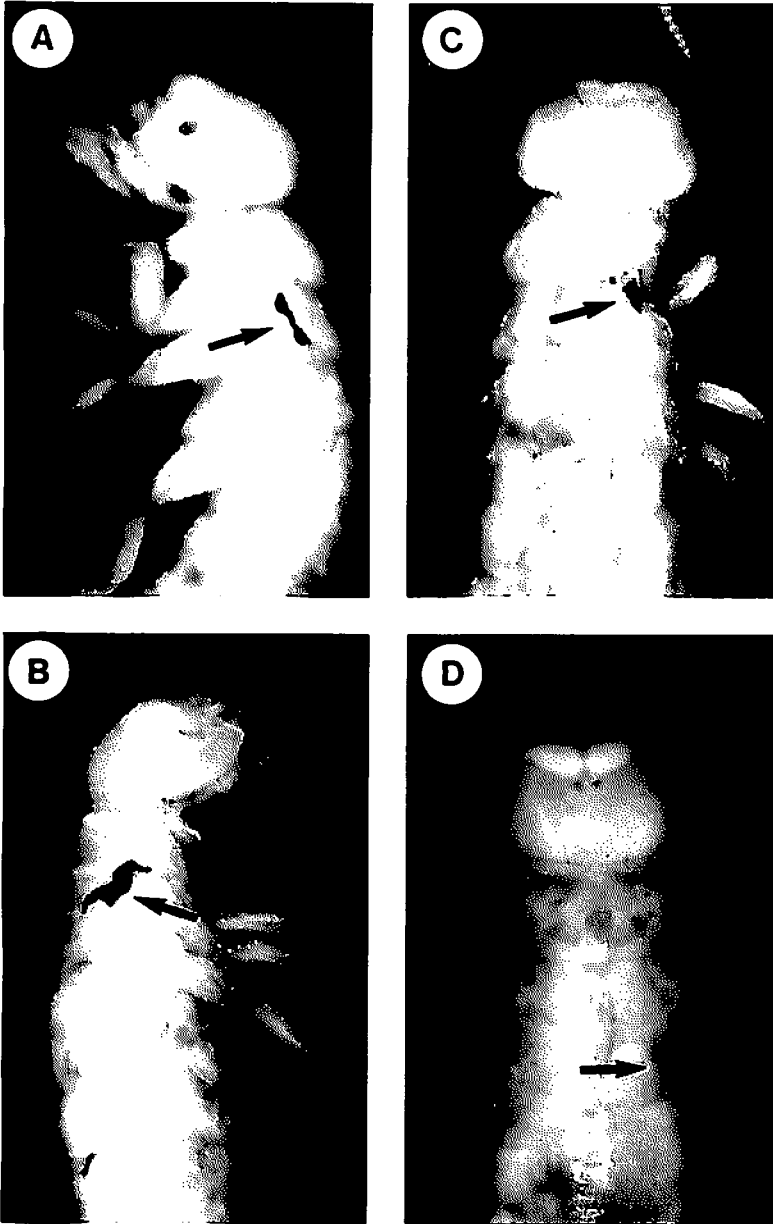


FIGURE 2. A, *Cryptotermiter brevif*: wing pad scar to left mesothoracic pad of nymph. B-D *Incisitermes immigrans*: B, scar to right mesothoracic wing pad of nymph; C, scar to pronotum and base of right mesothoracic wing pad of nymph; D, scar to right metathoracic wing pad of nymph.

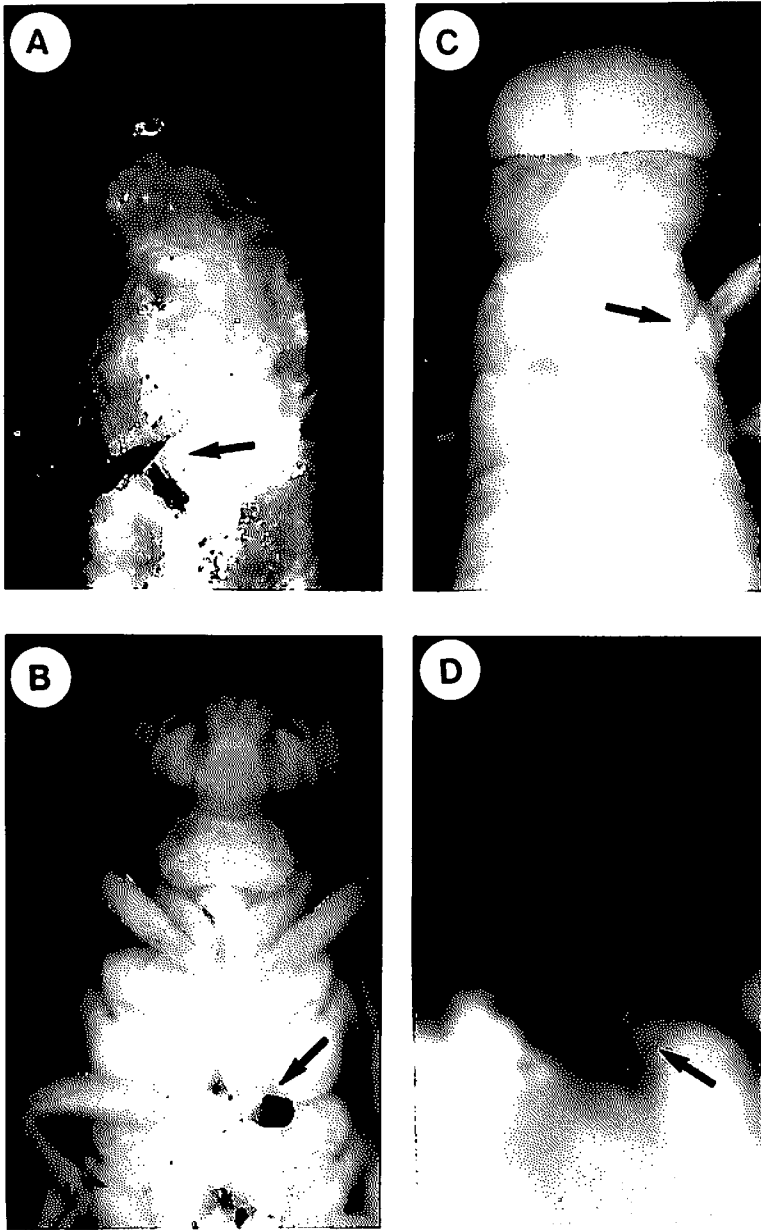


FIGURE 3. A-D *Neotermes connexus*: A, scars to left meso- and metathoracic wing pads of nymph; B, leg truncation scar to trochanter of left mesothoracic leg of nymph; C, asymmetrical wing pads of neotenic with right mesothoracic pad healed and regressed; D, regenerated right metathoracic leg stub.